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THE RESPIRATORY ADAPTATIONS OF THE PODIA AND AMPULLAE OF ECHINOIDS (ECHINODERMATA)[1]

DOUGLAS H. FENNER[2]

Reed College, Portland, Oregon 97202, and the Marine Biological Laboratory, Woods Hole, Massachusetts 02543

Early work on the structure of echinoid podia and ampullae consisted of verbal descriptions and line drawings (Bather, 1900; Chadwick, 1900; Ludwig, 1904; MacBride, 1909; Cuenot, 1948; Hyman, 1955), some of which were highly schematic. Nichols (1959a, 1959b, 1961) has made photomicrographs showing the wide variety of adaptations of the terminal suckers of several echinoids. Most recently, Kawaguti (1964, 1965), and Coleman (1969) have investigated the structure of the wall of the tube feet and ampullae of echinoids using electron microscopy. Because the podia are the primary respiratory structure of echinoids (Farmanfarmaian, 1959, 1966, 1968; Steen, 1965), a systematic search for respiratory adaptations in the structure of echinoid podia was undertaken (Fenner, 1971).

The podium-ampulla system of most echinoids differs from that of asteroids and holothuroids in two respects. First, the connection between the echinoid podium and ampulla consists of two pores through the body wall instead of one. Recently, Yoshida (1966), and Coleman (1969) showed a septum dividing the base of the tube foot of *Diadema,* each half of the lumen being served by one of the pair of pores through the body wall. An exception to the rule of two pores per podium is the arrangement found in the accessory tube feet on the oral surface of the sand dollar *Echinocyamus,* which have only one pore passing through the body wall (Nichols, 1959b). Secondly, the echinoid ampulla has been reported to be crossed by strands of tissue (Ludwig, 1904; Cuenot, 1948; Hyman, 1955), or septae (Kawaguti, 1965), unlike the asteroid or holothuroid ampulla.

The non-locomotor podia on the aboral surface of several echinoids (*Cidaris* and *Echinus:* Nichols, 1961; clypeastroids: Hyman, 1955; and spatangoids: Hyman, 1955, and Chesher, 1969) are believed to serve a respiratory function. Nichols (1959b) presented the histology of the respiratory podia (petaloids) of the clypeastroid, *Echinocyamus.* Ciliary currents within the podia contribute to respiratory gas transport (Faramanfarmaian, 1966). The spatangoids (Chesher, 1969) have a counter-flow between the ciliary currents within the podia and the ciliary currents outside the podia; such a counter-current should enhance exchange of gases across the surface of the respiratory podia.

This study was undertaken to systematically search for respiratory adaptations in echinoid podia and ampullae, and to clarify our knowledge of the morphology of echinoid podia and ampullae.

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[2] The author's present address is Psychology Department, University of Pennsylvania, Philadelphia, Pennsylvania, 19104.

MATERIALS AND METHODS

Specimens were obtained from Gulf Specimen Co., Dr. J. Morin, Dr. J. McCauley, B. Madden, Dr. R. Wiggley, Dr. H. Sanders, Dr. R. Fay, Dr. P. Kier, Dr. W. Durham, the Marine Biological Laboratory Supply Department, and the Smithsonian Institution. The taxonomy of the species studied is presented in Table I.

Ciliary currents were mapped by watching the movement of carbon particles outside of the podia and ampullae, and free-floating pigmented coelomyctes within podia and ampullae. For histology, living specimens were relaxed in 7% MgCl before podia were removed and fixed in 10% formaldehyde or Bouin's Fixative (Gurr, 1962). Decalcification was accomplished by the actic acid in the Bouin's, or 10% HCl after formaldehyde fixation. Tissues were dehydrated through a series of alcohols and embedded in parafin. Sections were cut at 8–15 microns and stained with Haematoxylin-Eosin (Gurr, 1962), Mallory's Haematoxylin (Grey, 1966), or Hubschman's (1962) modification of the Mallory triple connective-tissue stain.

TABLE I

The classification of the species studied, from Mortensen (1928–1951). Asterisk indicates living specimen studied

- Class Echinoidea
  - Sub-class Regularia
    - Order Echinothuroida
      - Family Echinothuridae
        - *Sperosoma giganteum*
        - *Phormosoma plascentei*
    - Order Cidaroida
      - Family Cidaridae
        - *Cidaris abysicola*
        - *Eucidaris tribuloides**
    - Order Stirodonta
      - Family Arbaciidae
        - *Arbacia punctulata**
        - *Tetrapygus niger*
      - Family Saleniidae
        - *Salenia goesiana*
      - Family Stomopheustidae
        - *Stomopneustes variolaris*
      - Family Phymosomatidae
        - *Glyptocidaris crenularis*
    - Order Camarodonta
      - Family Toxopneustidae
        - *Lytechinus variagatus**
        - *Tripneustes gratilla*
      - Family Temnopleuridae
        - *Salmacia alexandri*
      - Family Strongylocentrotidae
        - *Strongylocentrotus purpuratus**
        - *Strongylocentrotus droebachiensis**
        - *Allocentrotus fragilis*
    - Order Camarodonta (continued)
      - Family Echinidae
        - *Echnius affinis*
      - Family Echionometridae
        - *Echinometra mathei*
        - *Heterocentrotus mammilatus*
      - Family Parasaleniidae
        - *Parasalenia gratiosa*
    - Order Aulodonta
      - Family Diadematidae
        - *Centrostephenus coronatum*
      - Family Micropygidae
        - *Microgyga tuberculata*
      - Family Aspidodiadematidae
        - *Plesiodiadema indicum*
      - Family Pedinidae
        - *Caenopedina indica*
  - Sub-class Irregularia
    - Order Clypeastroida
      - Family Scutellidae
        - *Mellita quinquesperforata**
        - *Echinarachnius parma**
        - *Dendraster excentricus**
    - Order Spatangoida
      - Family Schizasteridae
        - *Brisaster latifrons*
      - Family Loveniidae
        - *Lovenia cordiformis*
      - Family Brissidae
        - *Brissopsis lyrifera*
      - Family Hemiasteridae
        - *Hemiaster expergitus*

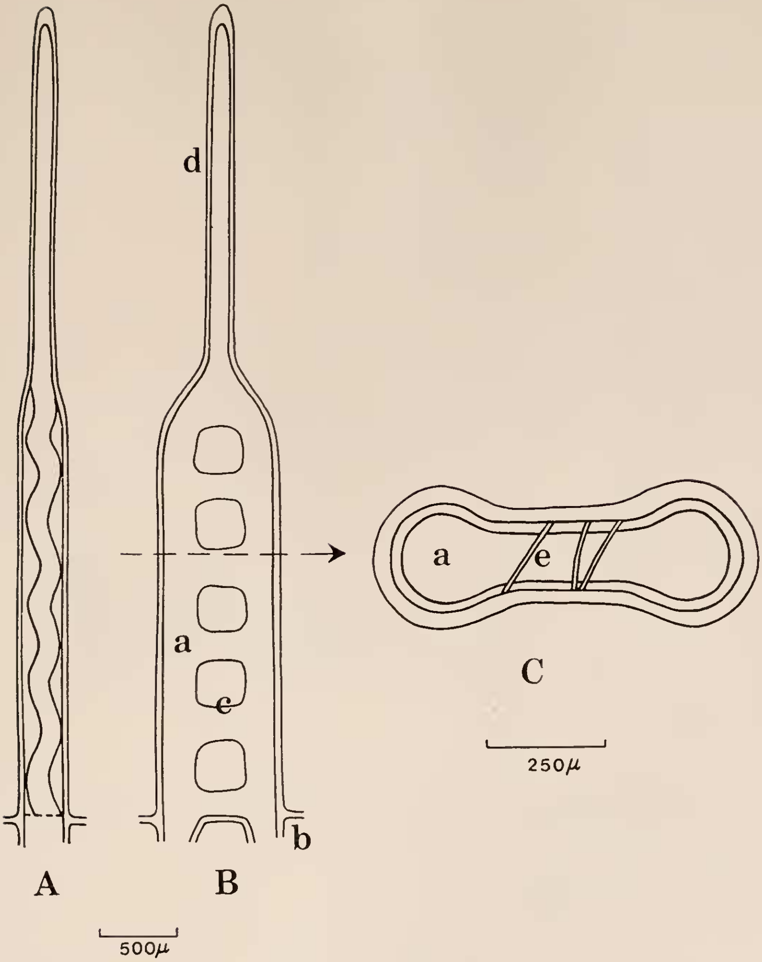

Figure 1. Respiratory podium of *Eucidaris tribuloides;* (A.) edge view; (B.) side view; (C.) cross section; (a.) marginal tube; (b.) test; (c.) thin, rippled area; (d.) distal tube; (e.) strands of connective tissue. The actual sizes of podia and ampullae vary considerably with the size of the animal, location of podia on animal, and state of contraction of podium.

Results

Order Echinothuroida

Two species in this order were examined: *Sperosoma giganteum* and *Phormosoma plascentei.* There are two pores in the body wall for each podium, and both podia and ampullae are hollow. Podia on the oral surface, which terminate in suckers, fit the classical description of tube feet (Bather, 1900; Chadwick, 1900; Ludwig, 1904; MacBride, 1909, Cuenot, 1948; Hyman, 1955). Podia on the aboral surface, while shaped like tube feet, terminate bluntly without a sucker.

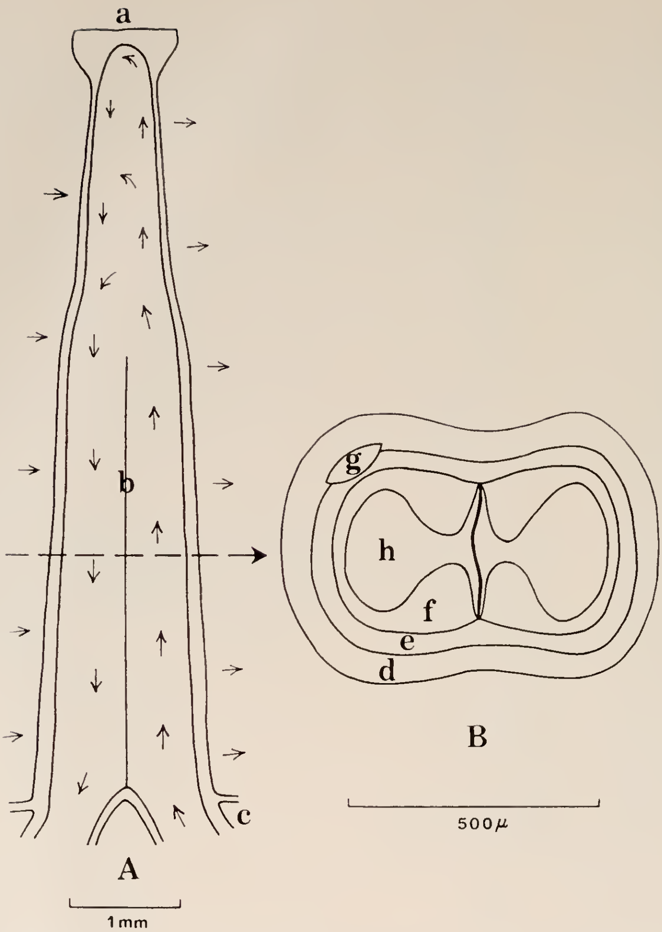

FIGURE 2. Tube foot of *Strongylocentrotus purpuratus;* (A.) whole tube foot seen from side; (B.) cross section from "double-barreled" region; (a.) sucker; (b.) septum; (c.) test; (d.) epithelium; (e.) connective tissue layer; (f.) muscle; (g.) nerve; (h.) lumen. Arrows indicate ciliary currents.

Order Cidaroida

Cidaris abyssicola and *Eucidaris tribuloides* have two types of podia, both served by pairs of pores in the test. Podia on the oral surface are hollow tube feet with terminal suckers. Podia on the sides and aboral surface are flattened, respriatory podia lacking suckers (Fig. 1). There is a channel along each edge and a thin, rippled area in between. The distal half is a thin, bluntly ending tube. The lumen is crossed by a few large strands of connective tissue. Often the respiratory podia are partially or wholly retracted beneath the ambulacral spines. When preserved without prior relaxation, these podia retract until they form a blunt triangle. The ampullae of *C. abyssicola* are flattened sacs, the lumen being crossed by septae, similar to the camarodont ampullae described below.

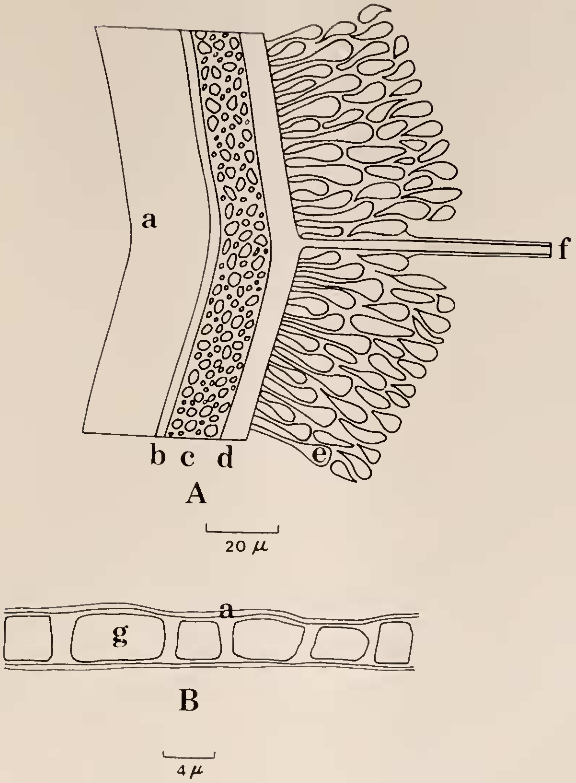

FIGURE 3. Details of the tube foot wall and septum of *S. purpuratus*. (A.) Detail of the junction of the connective tissue in the podial wall and the septum, from a cross section of the podium; (B.) detail of the septum sectioned parallel to the length of the tube foot; (a.) epithelium; (b.) outer, circular layer of connective tissue; (c.) middle, longitudinal layer of connective tissue; (d.) inner, circular layer of connective tissue; (e.) muscle cells; (f.) septum; (g.) cross section of strand of connective tissue.

Order Camarodonta

Families Strongylocentrotidae, Toxopneustidae, Temnopleuridae, and Echinidae. The seven members of these families that have been studied (*Strongylocentrotus purpuratus, S. drobachiensis, Allocentrotus fragilis, Lytechinus variagatus, Tripneustes gratilla, Salmacia alexandri,* and *Echinus affinis*) have virtually identical morphology and will be treated together.

In all seven species, there are two pores through the body wall for each tube foot. A septum, continuous with the wall separating the two pores of the test, runs halfway up the center of the podium (Fig. 2). In a cross section of the podium (Figs. 2B, 3A), it can be seen that the septum is continuous with a layer of tissue in the wall of the tube foot. The septum is continuous with the inner of the three adjacent layers of connective tissue in the wall of the podium (Fig. 3A). Each layer is made up of strands 2–6 microns in diameter. The inner and outer layers run circularly while those in the middle layer are longitudinal strands.

Strands in the septum form a single layer running across the lumen. A lightly staining layer less than one micron thick covers the septal strands and bridges the gaps between them (Figure 3B). The strands probably correspond to the bundles of collagen fibers, and the thin covering to the epithelium lining the podial lumen, which Kawaguti (1964) found in electron micrographs. Coleman (1969) found that the septum in the podia of *Diadema antillarum* consisted of collagen, a single cell layer thick. The buccal podia do not appear to have septae. Podia on the aboral surface have septae as described. The 8 podia nearest the aboral pole in each ambulacral row are so short that they do not project above the test. These have no septae or suckers. The most aboral 8 podia were examined closely only in *S. droebachiensis.*

The ciliary current within the tube foot moves toward the proximal end of the podium on the side nearest the radial canal, and toward the distal end on the other side (Cuenot, 1948). In the proximal half of the tube foot these two currents are separated by the septum, but in the distal half there is no dividing septum and mixing by eddies may occur. The ciliary current outside the tube foot moves across it, and thus does not run counter to the current inside.

The ampullae are flattened, leaf-like sacs that connect by way of the pore pairs to the podia and by way of a small tube (Fig. 5Ab) guarded by a one way valve (Nichols, 1966) to the radial canal. The ampullae lie like pages of a book, one row on each side of the radial canal in each ambulacrum. The distance separating adjacent ampullae is about equal to the thickness of one ampulla (about 0.2 mm). The pores pass through the test at angles up to 45°, such that the pores are closely adjacent to each other where they connect with the podium, but more widely separated where they connect with the ampulla. The lines seen within the ampulla correspond to septae connecting the walls (Figs. 4B, 4C). The septae consist largely of connective tissue, but the presence of muscular tissue could not be denied or confirmed. Only *A. fragilis* has ampullae that are connected to each other by strands attached to the outer edge of the ampullae.

The septae guide the ciliary currents within ampullae (Fig. 4B). The ciliary current outside the ampullae runs counter to that within the ampullae. This is true of flattened ampullae divided by septae in all species examined alive.

Families Echinometridae, Parasaleniidae. Echinometra mathei, Heterocentrotus mammilatus, and *Parasalenia gratiosa* have tube feet on their oral surfaces which are similar to those of members of the other camarodont families: they are tall, and each has a sucker and a septum. Strands in the septum of the podia of *P. gratiosa* are not connected by an epithelium, but elsewhere the lumen is lined with a thick epithelium covering the muscular layer. The aboral surface (and equatorial areas of *H. mammilatus*) has greatly shortened, slightly flattened podia with rounded distal ends lacking suckers. The presence or absence of septae or strands within these podia was not determined. All of the ampullae are similar to the other camarodonts.

Order Aulodonta

The four aulodont species studied (*Centrostephanus coronatum, Micropyga tuberculata, Plesiodiadema indicum,* and *Caenopedina indica*) have nearly identical podial morphology. Podia on the oral surface are suckered tube feet with septae, and closely resemble the tube feet of the oral surface of camarodonts. Podia on

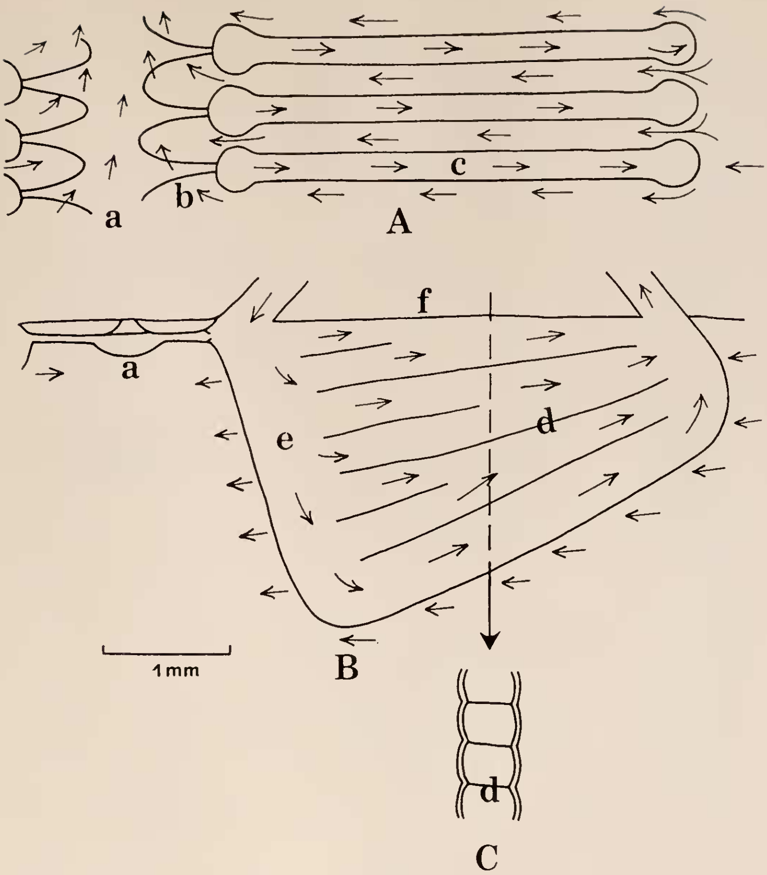

FIGURE 4. Ampullae of *S. purpuratus*; (A.) a row of ampullae lined up in the ambulacral areas as seen from the coelomic side of test; (B.) a single ampulla viewed from the side; (C.) cross section of the ampulla; (a.) radial canal; (b.) branch connecting radial canal and ampulla; (c.) ampulla; (d.) septae; (e.) marginal tube; (f.) test. Arrows indicate ciliary currents.

the aboral surface of all four aulodont species are bluntly-ending (no suckers), thin-walled podia with septae. The aboral podia are roughly as tall as the oral podia (and thus much taller than the aboral podia of the echinometrids and parasalenid studied).

The ampullae of two species, *C. coronatum* and *M. tuberculata*, were studied. Ampullae of both species consist of flattened sacs, the lumen of which is crossed by septae or "bands." In *M. tuberculatum*, "bands" crossing the lumen are arranged in definite rows.

Order Stirodonta

The only stirodont available alive was *Arbacia punctulata*, which will be discussed first. Specimens of *A. punctulata* have four types of podia. Nearest the

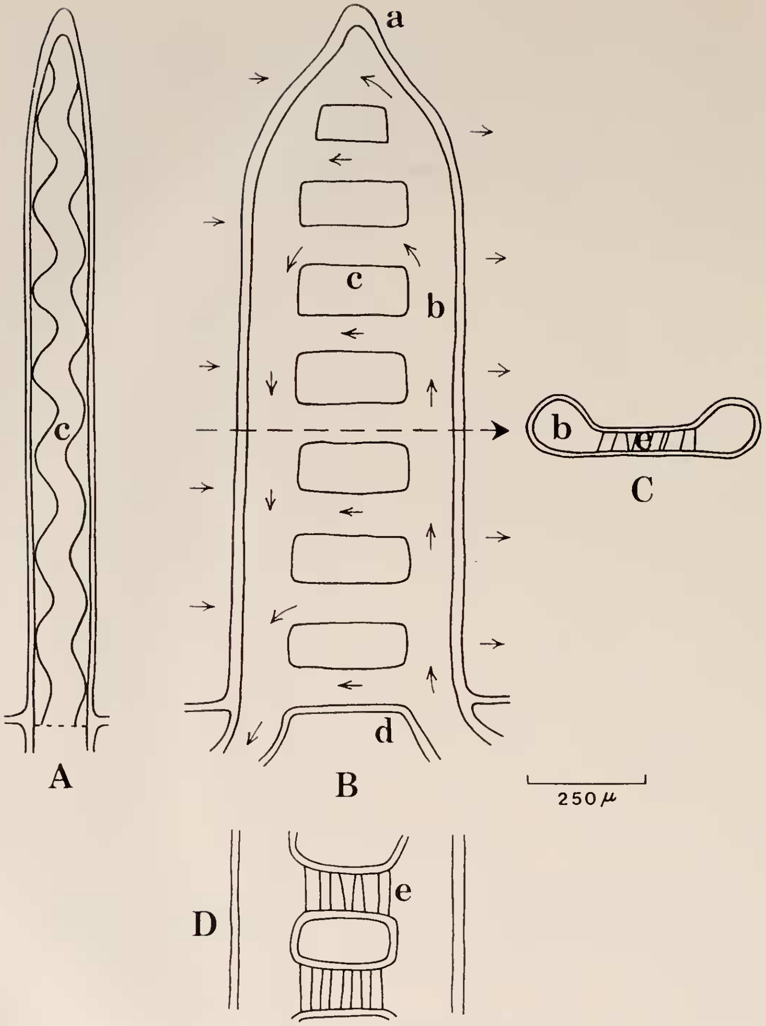

Figure 5. Respiratory podium of *Arbacia punctulata;* (A.) podium viewed from the edge; (B.) podium viewed from the side; (C.) cross section of the podium; (D.) longitudinal section of the podium; (a.) apex; (b.) marginal tube; (c.) thin, rippled area; (d.) test; (e.) strands of connective tissue. Arrows indicate ciliary currents.

aboral pole are flattened respiratory podia that lack suckers. At the animal's equator are long tube feet with small suckers, which may be sensory. These tube feet continually wave about, and do not attach to the substrate during locomotion. When they touch an individual of the same species, the animal locomotes away from the other individual. The buccal podia resemble the camarodont's buccal podia. The locomotor tube feet are located between the long podia and the buccal podia. The locomotor tube feet are moderately long (more so than the oral spines), have a large sucker, and no strands or septum.

The respiratory podia have two tubes, one running along each edge. The tubes are connected at the apex of the podium and by a thin, rippled area between the tubes (Fig. 5). Thus, a cross section in the middle of the petaloid is dumbbell-shaped (Fig. 5C). The two walls of the rippled area are held a fixed distance apart by thin strands of connective tissue crossing the lumen. Londitudinal sections show that the connective tissue is in the form of strands and not septae (Fig. 5D). Ciliary currents within the podium move toward the ampulla in the tube nearest to the radial canal and away from the ampulla on the other side. The current crosses the thin, rippled area along the arrows shown in Figure 5B. On the outside of the podium, the ciliary current passes across the podium counter to the current inside the thin, rippled area of the podium (Fig. 5B). The most aboral of these respiratory podia have a hollow tubular region on the distal end like those of the cidarids (Fig. 1).

The long, sensory podia have a small sucker, a hollow tubular section and a double-barreled section near the base. Instead of a septum, strands of connective tissue similar to those in the petaloids separate the two barrels near the base of the tube foot. In the sensory and locomotor podia, the ciliary currents within the tube foot move proximally on the side nearest the radial canal, and distally on the opposite. Some mixing between the two currents occurs. Each podium is served by two pores in the test.

The ampullae are also differentiated. All of the ampullae except those nearest the mouth closely resemble the camarodont ampullae (Fig. 4). The ten or so ampullae in a row nearest the mouth do not have septae, and are not flattened but irregular in shape. Unlike the other ampullae, those closest the mouth do not have their ciliary currents organized in a counter-current fashion.

Tetrapygus niger (also in family Arbaciidae) has hollow tube feet with suckers on its oral surface like *A. punctulata.* Some of the podia on the aboral surface closely resemble those on the aboral surface of *A. punctulata.* Others are more flattened and blunt on the distal end, but are crossed by strands like the rippled podia.

Salenia goesiana (family Saleniidae) has spines which closely resemble those of the cidarids: large primary spines surrounded by smaller spines, and two rows of spines between the two rows of podia in each ambulacrum. These latter spines are somewhat flattened and project over the podia. The preserved aboral podia are small and blunt, resembling the preserved podia of cidarids. The tube feet on the oral surface are hollow like those of the cidarids.

Stomopneustes variolarus and *Glyptocidaris crenularis,* in contrast to the previous stirodonts considered, have aboral tube feet with suckers, and all tube feet have septae like the camarodont podia.

Order Clypeastroida

Three species, all in family Scutellidae, were examined: *Mellita quinquesperforata, Dendraster excentricus,* and *Echinarachnius parma.* The podia of all three species are differentiated into two distinct types. Located on the aboral surface are large respiratory podia (petaloids) arranged in very definite ambulacral rows which in the cleaned test form five petals. The small (accessory) tube feet, however, are scattered throughout the ambulacral areas on the oral surface (most dense in the

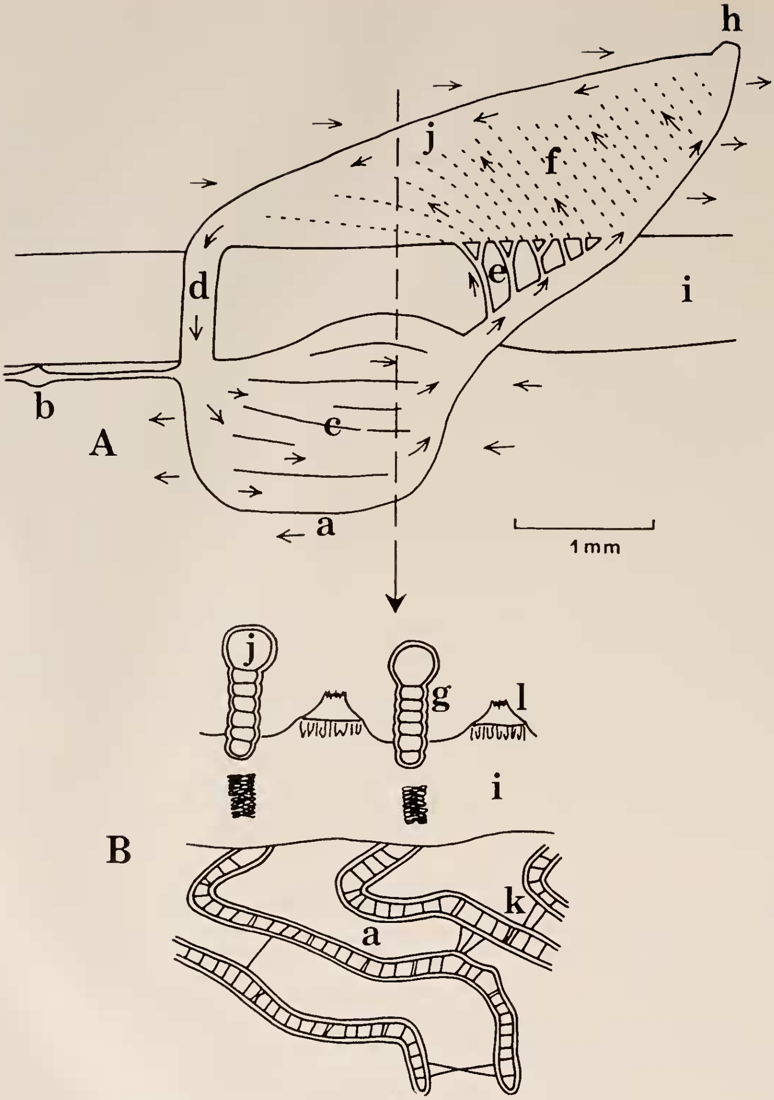

FIGURE 6. The respiratory podium and ampulla of *Dendraster excentricus;* (A.) viewed from the side; (B.) seen in cross section; (a.) ampulla; (b.) radial canal; (c.) septum; (d.) pore through the test; (e.) secondary pores through the test; (f.) rows of strands; (g.) petaloid (respiratory podium); (h.) knob; (i) test; (j.) marginal tube; (k.) strands connecting ampullae; (l.) bases of spines.

ambulacral grooves) and edges of the sand dollar. In *E. parma* and *D. excentricus* they exist on the aboral surface between the two rows of petaloids in each petal (ambulacral row). In that area only, they are arranged in rows in line with the petaloids. In *D. excentricus,* the ambulacral grooves of the oral surface continue around on the aboral surface as ridges: some running within the petals, some between.

The accessory tube feet of all three species are small, thin tubes terminating in adhesive bulbs such as in *Echinocyamus pusillus* (Nichols, 1959b). The largest accessory tube feet on *D. excentricus* have a sucker instead of a bulb on the end. The shaft has a hollow lumen served by a single pore in the test. No ciliary currents exist within or around the tube feet. However, coelomocytes (and thus the fluid in the lumen) move distally during extension of the tube feet, and proximally during their retraction.

The petaloids are long parallel to the test and protrude from the test as far as the spines between which they are found. The end farthest from the radial canal protrudes farthest from the test, and has a small lump resembling the adhesive bulb at the end of the accessory tube feet. A large tube runs along the top edge of the petaloid, and connects to the pore(s) farthest away from the radial canal by small "tubes" (Fig. 6). The lumen of the petaloid below the large tube is completely divided up into the small "tubes" by rows of strands of connective tissue. Nichols (1959b) reports that the petaloids of *Echinocyamus pusillus* are crossed by 4–8 strands per podium. Free-floating coelomocytes were never observed passing from one "tube" to another, but always moving within a single "tube." Thus, the rows of strands are quite effective in directing ciliary currents. The ciliary currents on the outside of the petaloid move away from the radial canal, counter to the current within the petaloid.

The passage of the tubes through the test was studied by breaking and examining cleaned, dried tests. The pore passing through the test nearest the radial canal is unitary, except in *D. excentricus*, where it may split into two as it approaches the inner surface of the test. In *D. excentricus* and *M. quinquesperforata* (*E. parma* was not closely examined), the pore farthest from the radial canal gives off one to eleven tubes on the side nearer the radial canal as it approaches the outer surface of the test (Fig. 6Ae). The same arrangement has been found in fossil scutellids (Schaffer, 1962). The ampullae serving the petaloids are flattened sacs divided by septae. In all three species, the ampullae are bent so as to lie at an angle, and are connected to each other by strands (Fig. 6B). Ciliary currents in the petaloids' ampullae move as in camarodont ampullae. The ampullae connected to the accessory tube feet are simple, round or elongated sacs, without septae. On the aboral surface of *E. parma* and *D. excentricus* they are located along the branch canals connecting the radial canal and petaloid ampullae. On the oral surface of these two species, these small ampullae are located on branches leading from the radial canal, many ampullae on each branch. In *M. quinquesperforata*, however, there are ampullae visible only on the branches nearest the mouth. Farther from the mouth the branches enter the test without ampullae attached to them. The branches pass horizontally for about 2–10 mm in the system of "microcanals" (Schaffer, 1962). Durham (1966) reports that Wagner found ampullae for the accessory tube feet within the microcanals of *Encope*. No ciliary currents were seen within or around any of the simple ampullae in the present study.

Order Spatangoida

The four species examined (*Brisaster latifrons, Brissopsis lyrifera, Hemiaster expergitus*, and *Lovenia cordiformis*) have nearly identical podial morphology and

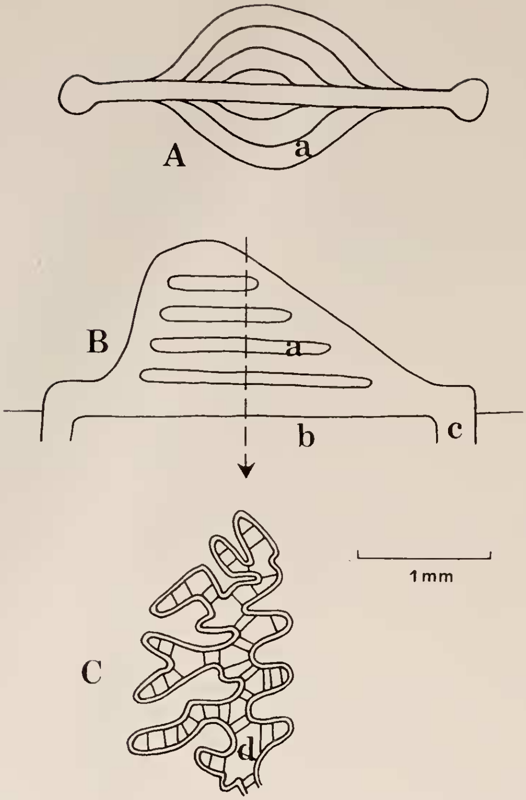

FIGURE 7. The resipratory podium of *Brisaster latifrons;* (A.) as seen from above; (B.) as viewed from the side; (C.) cross section; (a.) "lamellae" or "ripples"; (b.) test; (c.) pore through test; (d.) strands or septae.

will be treated together. Heat urchins (spatangoids) have highly differentiated podia. The tube feet of the anterior petal are used in building the respiratory tunnel to the surface of the substrate. Respiratory petaloids are found in the other four petals. Tube feet surrounding the mouth and anus are used in ingestion and building the drainage canals, respectively.

The tunnel-building tube feet of the anterior petal have a hollow lumen served by a pair of pores in the test. The ampullae connected to those tube feet are simple, hollow sacs. The oral and anal podia and their ampullae are similar to the tunnel-building tube feet, except they are each served by a single pore in the test.

The respiratory petaloids are triangular-shaped, stretched between their two pores. The sides of the larger petaloids are folded into "ripples" or "lamellae" (Fig. 7). The lamellae of *B. latifrons* and *B. lyrifera* alternate between the two sides (Fig. 7C), just as do the "ripples" of the cidarid and arbacid respiratory podia. The lamellae of *L. cordiformis* and *H. expergitus* are found on only one side of the petaloid, as shown for *Echinocardium cordatum* by Cuenot (1948).

Septae (or possibly rows of strands) consisting of connective tissue covered with epithelium divide the lumen and fix the separation of the walls. They probably channel the ciliary currents as in the clypeastroid petaloids. The petaloids are served by camarodont-type ampullae. The central area of some of these ampullae bend and fold out of the plane of the ampulla.

Discussion

In the variety of respiratory podia presented above, four principal adaptations are apparent which are absent in podia not specialized for respiration (*i.e.,* other podia in echinoids, podia of asteroids and holothuroids). First, there is the separation of the two ciliary currents within the podium; secondly the increase in surface area of the podia and ampullae; thirdly, the counter-current across the surfaces of podia and ampullae; and fourthly, the favorable positioning on the animal of podia specialized for respiration.

The separation of the ciliary current going from ampulla to podium from the return current is accomplished by the division of the pore passing through the test into two pores, each containing a single current. The great separation of the current entering the ampulla from that leaving is accomplished by the ampulla's flattened shape, and the current-guiding septae within. The currents entering and leaving the podium may be separated by a septum or by the flattened shape of the podium. In tube feet with septae, a counter-current across the septum may occur, reducing efficiency.

The surface area of some ampullae and podia is increased by their flattening. The podia of cidarids, arbacids, and spatangoids further increase their respiratory surface area by having their walls folded into ripples and lamellae. The walls of the flattened podia and ampullae are held together by the strands and septae of connective tissue which thus perform a function similar to the pillar cells in teleost (Hughes and Grimstone, 1965), and crustacean (Copeland, 1968) gill lamellae.

The ciliary currents inside and outside of flattened ampullae are arranged in a counter-current, as are the currents of flattened podia. The ciliary currents of tube feet with septae are not so arranged. Currents on the inside and outside of the podia move at right angles to each other. Ciliary currents provide the only ventilation of the highly specialized respiratory podia of the aboral surfaces of many echinoids. These podia are not used for locomotion, and (except for the cidarids) retract only if stimulated. Movement of the tube feet used for locomotion may contribute to ventilation.

The ciliary currents crossing the two rows of ampullae in an ambulacrum move from the inter-ambulacral area toward the radial canal, and then into the coelomic cavity. This is a more efficient arrangement than if the current passed over one row of ampullae, and then over the second before circulating into the cavity. After passing over one row of ampullae, the fluid has an increased oxygen content. If it then passed over the second row, the oxygen gradient across the (second row) ampullar walls would be less than if the fluid had not passed over the first row of ampullae before passing over the second row. The ciliary currents over respiratory podia are likewise advantageously arranged, and Paul (1968) has postulated a similar system for some fossil echinoderms.

The podia having the above three adaptations are invariably positioned favorably on the animal. Echinoids, with one known exception, keep their mouth toward the substrate, or pointed down if they burrow in the substrate. The flattened podia of cidarids, salenids, and arbacids are found on the aboral surface of these epifaunal species. The flattened podia of the clypeastroids and spatangoids are confined to the aboral surface of these infaunal species. By projecting away from the aboral surface, the respiratory podia miss the layer of oxygen-depleted water around the animal and its substratum. The single exception to the rule that all echinoids keep their mouth down or toward the substrate is the sand dollar, *Dendraster excentricus*. This sand dollar frequently "stands" on its anterior edge with that edge submerged in sand. It is eccentric such that the mouth and petals containing the respiratory podia are nearer the posterior (anus) than anterior edge. Thus, the resipratory podia are kept above the oxygen-poor sand.

The peristomeal gills of regular echinoids may be relatively undeveloped because they project down toward the substrate. The infaunal, irregular echinoids have no such peristomeal gills and depend entirely upon podia for respiratory structures. The podia of classes of echinoderms other than Echinoidea may not be anatomically specialized for respiration because alternative respiratory structures project upward into the water column.

It is not clear why *Stomopneustes variolaris, Glyptocidaris crenularis* and most camarodonts show no oral-aboral differentiation of podia. It seems likely that the suckered aboral podia are adequately efficient at respiration due to the septum, and in addition can function in locomotion. These suckered aboral podia may serve a food-catching function, may be used to cover the animal with objects for shade or camouflage, and/or serve to anchor the animal following dislodging before breakage by wave action can occur.

The type of ampulla is correlated with the resipratory specialization of the podium it serves. Thus, flattened podia and podia with septae have flattened ampullae with septae, but hollow tube feet have hollow ampullae. The single exception found is a few hollow tube feet on the oral surface of *Arbacia punctulata* which may have flat, septate ampullae. That the septae of the ampullae serve primarily to increase strength in protraction of locomotor tube feet is rejected by consideration of the spatangoids. Spatangoids (heart urchins) have flat, septate ampullae serving non-locomotor respiratory podia, and hollow ampullae serving tunnel-building, *etc.* tube feet, which require greater protraction force than respiratory podia.

None of the above discussion of increased respiratory efficiency of some podia due to several adaptations has been corroborated by actual measurements and comparisons of efficiency of the various podia. Many podia and other external surfaces have been shown to act as gas exchange surfaces even though they are not specialized for that purpose (Farmanfarmaian, 1966). The measurement of oxygen tensions at selected positions in and around podia and other respiratory structures might indicate the relative efficiency of those structures with and without separation of currents, presence of counter-currents, and other adaptations.

The septae and strands of podia and ampullae of all species examined have a common basic structure. All are composed of strands of connective tissue continuous with that in the wall of the podium or ampulla. The strands are sometimes

Table II

The affinities of echinoid groups as determined by podial and ampullar morphology. The position of the urechinids and pourtalesids was assigned on the basis of Hyman's (1959) report of one pore per podium. The group "irregularia" here excludes the urechinids and pourtalesids, as the "stirodonta" excludes the Stomopneustidae and Phymosomatidae, and the "camarodonta" excludes the Echinometridae and Parasaleniidae

I. One pore in body wall per podium
    Urechinidae
    Pourtalesiidae
II. Two pores in body wall per podium
    A. No septae in ampullae
        Echinothuroida
    B. Septae in ampullae
        1. Strands in aboral podia
            Cidaroida
            Stirodonta
            Irregularia
        2. Septae in podia
            a. Aboral podia without suckers
                Aulodonta
                Echinometridae
                Parasaleniidae
            b. Suckered aboral podia
                Phymosomatidae
                Stomopneustidae
                Camarodonta

arranged closely in rows, forming septae. Many, possibly all, septae and strands are covered with an epithelium. The strands and septae probably have a common point of origin in the ancestors of the cidarids. The podial septae probably originated in the condensation into a continuous septum of the linear arrangement of strands in the sensory podia of ancestral stirodonts. The podia morphology of the echinoids diverged with time, the most highly adapted respiratory podia being present in those forms burrowing in the relatively anaerobic substrate.

The morphology of echinoid podia are of taxonomic importance. The affinities of the echinoids as based solely on podial and ampullar morphology can be seen in Table II. The echinothurids have the simplest morphology of all regular echinoids. The echinothurids are not similar to the aulodonts as predicted by Durham and Melville (1957). If the Diadematidae and Pedinidae have converged during evolution as Philip (1965) suggested, they have converged in podial morphology as well as lantern structure, *etc.*

The podial morphology of the aulodonts is mid-way between that of the stirodonts and the camarodonts, not between the cidarids and stirodonts as Durham and Melville's (1957) classification would predict. It seems likely that the aulodonts diverged from the stirodont stock that originated the podial septum. From that same stirodont stock, a different, divergent line developed aboral, suckered tube-feet in the phymosomatids and stomopneustids, and then echinoid-type plates and a camarodont lantern in the temnopleurids. This implies that the short, blunt aboral podia of the echinometrids and parasalenids are "degenerate," while the tall, blunt aboral podia of aulodonts are "primitive." Mortensen's (1928–1951) classification most nearly predicts the podial affinities found.

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SUMMARY

1. The morphology of the podia and ampullae of thirty echinoids spread over 7 orders is described.

2. Four adaptations for respiration are found in the podia and ampullae of echinoids. The first is the separation of ciliary currents in the podium-ampulla lumen by two pores in the body wall, a septum in some podia, and the ampulla's flattened shape. The ampullae are crossed by septae.

3. The second respiratory adaptation is an increase in surface area of ampullae and podia by flattening. Cidarids, arbacids, and spatangoids further increase podial surface area by folding.

4. The ciliary currents inside and outside of ampullae and some podia move in a counter-current, increasing respiratory efficiency.

5. The fourth adaptation for respiration is that all podia having the first three adaptations are favorably positioned on the animal for respiration. Ampullae adapted for respiration serve podia adapted for respiration.

6. All strands and septae crossing echinoid podial or ampullar lumina contain strands of connective tissue.

7. Mortensen's (1928–1951) classification most nearly predicts the podial affinities found.

LITERATURE CITED

Bather, F. A., 1900. *The Echinoderms.* Pages 1–344 in R. Lankester, Ed., *A Treatise on on Zoology, Volume 3.* Adam and Charles Black, London.

Chadwick, H. C., 1900. *Echinus. Memoirs of the Liverpool Marine Biological Society,* **3**: 1–28.

Chesher, R. H., 1969. *The Systematics of Sympatric Species of West Indian Spatangoids: A Revision of the Genera Brissopsis, Plactholaenia, Paleopneustes, and Savinaster.* Studies in Tropical Oceanography No. 7, University of Miami Press, Miami, 168 pp.

Coleman, R., 1969. Ultrastructure of the tube foot wall of a regular echinoid, *Diadema antillarum* Philippi. *Z. Zellforsch. Microsk. Anat.,* **96**: 162–172.

Copeland, D. E., 1968. Fine structure of salt and water uptake in the land crab, *Gecaricinus lateralis. Amer. Zool.* **8**: 417–432.

Cuenot, L., 1948. Antomine, ethologie, et systematiques des echinoderme. Pages 1–363 in P. Grasse, Ed., *Traite de Zoology, Volume 11.* Masson, Paris.

Durham, J. W., and R. V. Melville, 1957. A classification of echinoids. *J. Paleontol.,* **31**: 242–272.

Durham, J. W., 1966. Classification. Pages 270–295 in R. C. Moore, Ed., *Treatise on Invertebrate Paleontology, part U, Echinodermata 3.* Geological Society of America, New York.

FARMANAFARMAIAN, A., 1959. Respiratory surface of the purple sea urchin (*Strongylocentrotus purpuratus*). *Doctoral dissertation, Stanford University,* California, 98 pp.

FARMANFARMAIAN, A., 1966. Respiratory physiology of echinoderms. Pages 245–266 in R. A. Boolootian, Ed., *Physiology of Echinodermata.* John Wiley, New York.

FARMANFARMAIAN, A., 1968. The controversial echinoid heart and hemal system- function effectiveness in respiratory exchange. *Comp. Biochem. Physiol.,* **24**: 855–863.

FENNER, D. H., 1971. A comparative study of the respiratory adaptations of the podia of echinoids. *Biol. Bull.,* **141**: 385–386.

GREY, F., 1954. *The Microtomist's Formulary and Guide.* The Blakiston Co., Inc., New York, 794 pp.

GURR, E., 1962. *Staining: Practical and Theoretical.* The William and Wilkins Company, Baltimore, 631 p.

HUGHES, G. M., AND A. V. GRIMSTONE, 1965. The fine structure of the secondary lamellae of the gills of *Gadus pollachius. Quart. J. Microscop. Sci.,* **106**: 343–353.

HUBSCHMAN, J. H., 1962. A simplified azan process well suited for crustacean tissue. *Stain Tech.,* **37**: 379–353.

HYMAN, L. H., 1955. *The Invertebrates: Volume IV Echinodermata.* McGraw-Hill Book Company, New York, 763 pp.

KAWAGUTI, S., 1964. Electron microscopic structures of the podial wall of an echinoid with special references to the nerve plexus and muscle. *Biol. J. Okayama Univ.,* **10**: 1–12.

KAWAGUTI, S., 1965. Electron microscopy on the ampulla of the echinoid. *Biol. J. Okayama Univ.,* **11**: 75–86.

LUDWIG, H. VON, 1904. *Die Seeigel.* Pages 967–1345 in H. C. Bronn, Ed., *Klassen und Ordnungen des Their-Reichs, Band II, Abtheilung 3, Buch 4.* Verlagshandlung, Leipzig.

MACBRIDE, E. W., 1909. *Echinodermata.* Pages 1–623 in W. F. Harmar, and A. E. Shipley, Eds., *Cambridge Natural History, Volume I.* Macmillan and Company, London.

MORTENSEN, T., 1928–1951. *A Monograph of the Echinoidea: Volumes I–V.* Milford, Oxford University Press, London, 4472 pp.

NICHOLS, D., 1959a. The histology and activities of the tube-feet and clavulae of *Echinocardium cordatum. Quart. J. Microscop. Sci.,* **100**: 73–87.

NICHOLS, D., 1959b. The histology and activities of the tube-feet of *Echinocyamus pusillus. Quart. J. Microscop. Sci.,* **100**: 539–555.

NICHOLS, D., 1961. A comparative histological study of the tube-feet of two regular echinoids. *Quart. J. Microscop. Sci.,* **102**: 157–180.

NICHOLS, D., 1966. Functional morphology of the water-vascular system. Pages 219–244 in R. A. Boolootian, Ed., *Physiology of Echinodermata.* John Wiley, New York.

PAUL, C. R. C., 1968. The morphology and function of dichoporite pore-structures in cystoids. *Palaeontology,* **11**: 697–730.

PHILIP, G. M., 1965. Classification of echinoids. *J. Paleontol.,* **39**: 45–62.

SCHAFFER, H., 1962. Die scutelliden des miozans von Osterreich und Ungarn. *Palentol. Z.,* **36**: 135–170.

STEEN, J. B., 1965. Comparative aspects of the respiratory gas exchange of sea urchins. *Acta Physiol. Scand.,* **63**: 164–170.

YOSHIDA, M., 1966. Photosensitivity. Pages 435–464 in R. A. Boolootian, Ed., *Physiology of Echinodermata.* John Wiley, New York.